Mechanical Properties of Cat Soleus Muscle Elicited by Sequential Ramp Stretches: Implications for Control of Muscle

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SUMMARY AND CONCLUSIONS

1. Force changes in areflexive cat soleus muscle in decerebrate cats were recorded in response to two sequential constant velocity (ramp) stretches, separated by a variable time interval during which the length was held constant. Initial (i.e., prestretch) background force was generated by activating the crossed-extension reflex, and stretch reflexes were eliminated by section of ipsilateral dorsal roots.

2. For the initial 400–900 μm of the first stretch, the muscle exhibited high stiffness, classically termed "short-range stiffness." This high stiffness region was followed by an abrupt reduction in stiffness, called muscle "yield," after which force remained at a relatively constant level, achieving a plateau in force. This plateau force level depended largely on stretch velocity, but this dependence was much less than proportional to the increase in stretch velocity, in that a 10-fold increase in velocity produced <2-fold increase in plateau force.

3. In experiments where the velocities of the two sequential ramp stretches were identical, the force plateau level was the same for each stretch, regardless of the time elapsed before the second stretch (varied from 0 to 500 ms). In contrast, measures of stiffness during the initial portion of the second stretch showed time-dependent magnitude reductions. However, stiffness recovered quickly after the first stretch was completed, returning to control values within 30–40 ms.

4. In one preparation, in which the velocities of the two sequential ramp stretches were different, the force plateau elicited during the second stretch exhibited velocity dependence comparable with that recorded in the earlier single velocity studies. Furthermore, muscle yield was still evident in the case where the force change was due solely to the change in velocity and where short-range stiffness had not yet recovered fully from the initial stretch. On the basis of these findings, we argue that the classical descriptions of short-range stiffness and yield are inadequate and that the change in force that has typically been called the muscle yield reflects a transition between short-range, transient elastic behavior to steady-state, essentially viscous behavior.

5. To examine changes in the muscle's mechanical stiffness during single ramp stretches, a single pulse perturbation was superimposed at various times before, during, and subsequent to the constant velocity stretch. The force increment elicited in response to each pulse decreased relative to the initial isometric value, remained essentially constant until the end of the ramp, and then returned to its prestretch magnitude shortly (30–40 ms) after stretch termination. These findings indicate that shortening muscle sustains a reduction in stiffness during a ramp stretch.

6. These results have important implications for the neural control of shortening muscle. First, after stretch, areflexive soleus muscle quickly regains its initial stiffness, thereby resetting the muscle to a predictable and consistent mechanical state, a necessity if predictive control mechanisms are used to preserve elastic behavior. Second, because the steady state force generated by lengthening muscle is dependent largely on the velocity of stretch (and not on prior perturbation history) for a given initial force, the mechanical properties of muscle in the "post-yield" phase are largely analogous to those of a viscous damper. Third, it appears that stretch reflex compensation changes the basic form of the muscle's mechanical stiffness from one dominated by viscouslike behavior to one dominated by elastic behavior.

INTRODUCTION

The application of constant velocity (ramp) stretches to determine the mechanical stiffness of contracting muscle and of related stretch reflex actions has proven to be useful in a number of major studies (Joyce et al. 1969; Liddell and Sherrington 1924; Nichols and Houk 1976). The results of such ramp stretch studies are important in at least four respects.

First, stiffness measurements reflect the intrinsic ability of muscle and of superimposed reflex mechanisms to resist perturbations or to slow and eventually stop voluntary movements. The term stiffness is used throughout this paper in reference to the measurement of the net forces generated in response to an imposed length change, including all viscoelastic forces, such that

$$\Phi = \Delta F/\Delta \lambda$$

where $\Phi$ is the stiffness and $\Delta F$ and $\Delta \lambda$ are in units of force and length, respectively. Second, the prominent nonlinearities in the mechanical properties of muscle that are evident during stretch (see below) are important plant properties that the neuromuscular controller must take into account.

Third, the idea that stiffness may be a regulated variable of the nervous system has largely arisen from these types of perturbation experiments (Hogan 1990; Houk 1979; Stein 1982). Fourth, the characterization of these nonlinearities provides important constraints for developing various muscle models, and the simulation of experimentally recorded nonlinearities provides an excellent test of muscle model validity.

One of the most prominent nonlinearities seen during a stretch and of particular interest in the present study is muscle "yield," which has been described in a variety of preparations, including frog single muscle fibers (Flitney and Hirst 1978; Harry et al. 1990; Lombardi and Piazzesi 1990; Sugi 1972), cat whole muscle preparations (Joyce et al. 1969; Nichols and Houk 1976; R. F. Kirsch and W. Z. Rymer, unpublished data), and human muscle (Carter et al. 1990). The classical description of "yielding" is as follows. Initially, the force response to a constant velocity stretch is
essentially elastic, until the length change exceeded the "short-range stiffness region," which is usually between 0.5 and 1 mm of length change for cat soleus muscle (Walmsley and Proske 1981; Kirsch and Rymer, unpublished data). The subsequent force response is highly variable, depending on many factors such as the velocity of stretch and the level of neural activation, but a consistent feature is that the rate of force rise is sharply reduced after yield. The most commonly accepted explanation for muscle yield is that the balance between cross bridge attachment and detachment rates, as defined in the model of Huxley (1957) and Huxley and Simmons (1971), drastically shifts toward the detached state, once the maximum length over which a cross bridge can remain attached is exceeded (Harry et al. 1990; Joycc et al. 1969; Zahalak 1981).

The transition of muscle from an actuator having essentially elastic characteristics with high stiffness to one with sharply reduced stiffness has led some investigators to imply that yielding is a potentially destabilizing effect (Houk et al. 1981; Nichols and Houk 1976). These investigators argue that this prominent nonlinearity manifested during yield requires compensation, presumably by the stretch reflex, because the muscle can no longer resist perturbations in a springlike manner. Yet, the characteristics of the postyield mechanical properties of whole muscle have not been adequately described to determine whether postyield muscle can form a stable interface with loads. Certainly, the muscle's force-generating capabilities are reduced, but this does not automatically represent a form of unstable behavior.

The yielding of muscle is especially important for understanding reflex compensation. For many stretch velocities, the onset of yield is so rapid that it would be already evident by the time that classical feedback mechanisms are able to act. Yet it has been shown that when the stretch reflex is intact, yielding is not apparent, except at high stretch velocities, or at very high initial forces. Moreover, the reflex contribution is such that the total force response increases almost linearly as the stretch continues, thus the mechanical behavior remains essentially elastic (Nichols and Houk 1976). The fact that yield is not normally detectable indicates that alternative forms of compensation, such as predictive or anticipatory actions of reflex pathways are likely to be involved (Houk et al. 1981). Such schemes need the knowledge of plant characteristics to be successful, thus studying the relationship of stiffness to time and movement history dependence is important.

The aim of our experiments was to characterize the mechanical properties of the cat soleus physiologically activated with the crossed-extension reflex, during and subsequent to a yield caused by a constant velocity stretch. We observed that as the stretch continued after yield, the force response reached a plateau, so that the response was analogous to that of a viscous damper. In addition, by applying sequential ramp stretches separated by a variable time interval, the time course of restoration of both short-range stiffness was found to be rapid (30-40 ms). In separate experiments we further observed that the force response to brief length pulses, an alternative measure of muscle stiffness, fell during ramp stretch and that the stiffness remained near its minimum value throughout the duration of the stretch. These results are important for understanding the interactions between muscle and reflex/neural control mechanisms and are also important for our understanding of the intrinsic physiology of elongating muscle.

**METHODS**

**Decerebrate cat preparation**

Five adult cats of either sex, weighing 4-6 kg, were first anesthetized by a mixture of halothane, nitrous oxide, and oxygen and mounted in a surgical frame for fixation of the head, spine, pelvis, and left leg. The left soleus muscle and its innervation were dissected free from the surrounding tissue, and leg skin flaps were pulled up around the muscle to form a mineral oil pool. The temperature of the pool and muscle was maintained at ~35°C by heat lamps. The distal end of the tendon connected to the soleus was cut from the calcaneum, leaving a small bone chip. The tendon, with bone chip included, was then fixed to a 25-lb. load cell (Sensotec), which was attached in series to a linear motor. Motor position and muscle length were measured by a linear variable differential transformer (LVDT). The motor was configured as a length servo (internal compliance ~0.015 mm/N).

The decerebration was accomplished by sectioning the brain stem just rostral to the superior colliculus with a fine spatula. The anesthetic was then withdrawn and a period of 30 min allowed to eliminate the effects of the anesthesia. A pair of Teflon-coated stainless steel wire electrodes (0.003 in. diam), bared over the terminal 10 mm, were inserted into the two ends of the muscle with hypodermic needles, allowing electromyographic (EMG) recordings to be made. After a lumbar laminectomy, the dorsal roots innervating the hindlimb muscles (L5-S1) were sectioned, and the absence of the stretch reflex was tested by vibrating the tendon, which would produce a reflex EMG response if the roots were partially intact. No such response was elicited.

**Experimental protocol**

During the experiment the signals from the LVDT, the load cell, and an EMG amplifier were low-pass filtered to prevent aliasing (cutoff at 400 Hz, 4-pole Butterworth) and then recorded on a PDP 11/73 computer at 1-kHz sampling rate. The muscle length was controlled via a D/A signal sent from the computer to the motor servo-amplifier.

The crossed-extension reflex, which was elicited by manipulation of the contralateral hindlimb, was used to activate the soleus muscle to a background force of 5 N. It was usually possible to hold this background force steady for the 2-s time period required of the experiments. Once the force was held steady at 5 N, the length perturbation was applied.

Two types of length perturbations were used. The first type consisted of two ramps of 2-mm amplitude each, separated by a variable time interval ranging from 0 to 500 ms between the end of the first ramp and the onset of the second ramp. The velocities of the first and second ramps were usually the same and ranged from 10 to 100 mm/s. In one animal additional studies were performed in which the two stretches were of different velocities. The second type of perturbation involved a series of trials where a single pulse was superimposed on a single ramp of 2 or 4 mm amplitude. The pulse was produced by adding a rectangular pulse of 4 ms in length to the D/A ramp signal at the appropriate time, and the resulting pulse was ~1 mm in amplitude, superimposed onto the original ramp perturbation. The time of the pulse within the stretch was systematically varied from trial to trial, with the onset of the pulse ranging from 5 ms after the onset of the stretch to 40 ms after the end of the stretch.

Ideally, it would have been preferable to evaluate the effects of successive ramps of similar or differing velocities over a range of
different starting lengths. Practically, we were constrained to begin our ramp stretches from 10 to 7 mm shorter than physiological maximum. This is because starting at shorter lengths made it difficult to sustain the required initial force level of 5 N, whereas starting at longer lengths raised the risk of overextending the muscle, and the forces generated at very long lengths contained a larger passive component. Isometric length tension data taken in some of the preparations showed the experiments were performed on the ascending limb of the length tension curve, approaching the plateau region.

**Processing of data**

The force level after the sharp decline in the rate of force rise was assessed by simply calculating the mean value of force in the interval from a specified point in time after the yield to 5 ms before the end of the ramp. The beginning of this time interval was determined by examining the derivative of force with respect to time, calculated by taking the difference of successive force data points in time and dividing by the sampling interval (1 ms). The difference record was then filtered forward and backward by a low-pass 10th-order FIR filter with a 100-Hz cutoff with the use of the MAT LAB software package. Next, the start of averaging interval was defined as the point of sharp decrease in the rate of force rise, quantitatively defined as the point in time satisfying the conditions

\[ |(\Delta F/\Delta t)_i - (\Delta F/\Delta t)_{i-1}| \leq 0.2 \times (\Delta F/\Delta t)_{\text{max}} \]  

and

\[ |(\Delta F/\Delta t)_i - (\Delta F/\Delta t)_{\text{max}}| \leq 0.2 \times (\Delta F/\Delta t)_{\text{max}} \]  

where \( F \) is the force, \( t \) is time, \( (\Delta F/\Delta t)_i \) is the derivative at sample \( i \), and \( (\Delta F/\Delta t)_{\text{max}} \) is the maximum of that derivative during the ramp. The selection of 20% of the maximum derivative in Eqs. 2 and 3 was an arbitrary choice. The idea was to develop a consistent and readily applicable definition of an interval during which the force response was relatively flat (Eq. 2) and presumably in steady-state, i.e., after the transients due to the yield had subsided (Eq. 3). Higher order derivatives may have been helpful but were sensitive to noise in the data. The start of this steady-state interval, as defined by Eqs. 2 and 3 was always well before the end of the ramp.

In addition, the postyield steady-state response was fitted by the equation

\[ F(t) = B \times v + K \times L(t) \]  

where \( F(t) \) and \( L(t) \) are the force and length recorded at time \( t \) respectively, \( B \) is the viscous coefficient, \( v \) is the velocity of stretch (a constant in our experiments), and \( K \) is the elastic coefficient. The \( K \) was determined to estimate whether the plateau region of the force response was flat during increasing length; in other words it estimated the magnitude of any elastic component.

**Results**

**Force response to constant velocity perturbations**

Figure 1 illustrates the force response of the cat soleus muscle to constant velocity stretches, with velocities of 100 and 20 mm/s and an amplitude of 4 mm. In all the experiments recorded, the muscle was first activated reflexively to reach a steady background force of 5 N and then stretched. The force produced by the muscle rose steeply during the initial portion of the stretch, indicating a region of high stiffness. After ~0.5 mm of stretch, the rate of rise of force dramatically decreased, as shown in the \( \Delta F/\Delta t \) record, producing the force response that has been classically called a yield, similar to that reported in other earlier studies in cat and frog (cited earlier). The yield was followed by a plateau in force, which continued until the end of the stretch. The start of the steady-state force interval is indicated by the dashed lines and arrows, which were drawn in accordance with the criteria of Eqs. 2 and 3. Once the new isometric length was reached, the force declined in an exponential-like manner and attained a near constant level that was dependent on the muscle length.

The plateau force achieved in the steady state was dependent primarily on the velocity of the stretch. Figure 2 illustrates the relationship between force and stretch velocity for two of the cats tested. As shown in Fig. 1, the steady-state force level reached during the stretch remained relatively constant. The constancy in force after yield was analyzed for all speeds in four of the cats tested, and these results are shown below. For slower stretch velocities, the force plateau achieved after yield showed more variation (Fig. 1B).

The force variation may cause two problems in calculating the average force during the force plateau. First, as the velocity decreased, the increase in the force derivative, \( \Delta F/\Delta t \), was not as steep. Second, the measurement of the force plateau for the slower velocities was more difficult, because the force increment was not much greater than the baseline isometric force. Also there was a greater tendency for force variation to occur, because the probability of spontaneous variation in the crossed-extension reflex was increased because of the longer time period of stretch. As a consequence, the percentage error in the plateau measurement was greater for the slower velocities.

The force response during the plateau was also analyzed by fitting Eq. 4 to the force and length data to quantify the degree of constancy of the steady-state response. The values of \( K \) (slope of force vs. length), of the single 4-mm ramps along with the 95% confidence intervals are reported in Table 1 for all the velocities of the preparations analyzed. The confidence intervals are all very small, the largest value being equal to 0.0352 N/mm, showing that the data are well modeled by the equation. For two of the preparations (3 and 4), the values of \( K \) are very small, indicating that elastic contribution little to the total force response over the 4-mm stretch. For the other two preparations (5 and 6), the elastic contribution is larger at the slowest velocities but does not contribute much at the highest speed.

**Application of second stretch**

Two stretches of 2-mm amplitude each and the same velocity were applied successively, separated by a variable time interval (Fig. 3). The purpose of the second stretch was to determine whether prior mechanical history affects the magnitude or time course of the muscle response, specifically the initial portion of the force response and the development of a force plateau. In Fig. 3, the second stretch produced a similar response to the first stretch, namely a steep increase in force, followed by a sharp decrease in the rate of force increase and a subsequent plateau in force. Qualitatively, this gross mechanical response did not change with the time of application of the second stretch, although there were changes in the time course of force increase. Specifically, there were systematic changes in the slope of the force increase to reach the plateau level, as...
FIG. 1. Response of areflexive muscle to a constant velocity stretch applied at (A) 100 mm/s and (B) 20 mm/s with an amplitude of 4 mm. Records shown are averages of 2 trials. The muscle was initially activated by the crossed-extension reflex to a background force of 5 N. The length was measured with 0 defined as the maximum physiological length. \( \frac{dF}{dt} \) was calculated as described in METHODS. Dashed line and arrow represent the start of the steady-state response as determined by the criteria of Eqs. 2 and 3.
shown in the $\Delta F/\Delta t$ record, and these changes depended on the recent history of length change (see further below).

One measure of the force response to the second stretch is the plateau level of the force achieved in the steady state, which is plotted in Fig. 4 for three different velocities of stretch, imposed in one animal. The plateau force level did not depend on the time interval between stretches, shown by the slope of the linear regression of force versus time in Fig. 4 for all three velocities shown not differing significantly from zero ($P < 0.025$). The slope was also tested for all five preparations and velocities used, and the results were similar to those shown in the figure, in that the slope of the regression was not significantly different from zero. Thus the force plateau achieved after yield was dependent only on the stretch velocity and not any prior mechanical events.

In one preparation the second stretch was applied to the muscle at a different velocity from the first stretch (Fig. 5). The mean values of plateau forces achieved for the two protocols, (one where the 2 stretches were of the same velocity and the other where they were different), are summarized in Table 2. For all the velocities of the second stretch, the averages from both sets of experiments were close; thus the velocity of the first stretch did not influence the plateau response of the second stretch.

As can be seen in Fig. 5A, when the velocity was increased (from 20 to 100 mm/s), a new plateau force level was quickly reached, which was similar in magnitude to that elicited by a control stretch applied 500 ms after the completion of the first stretch. Similarly, as shown in Fig. 5B, when the velocity decreased (from 100 to 20 mm/s), the force level decreased to a new level appropriate for the new velocity. In both figures the striking characteristic is that the relationship between steady-state force level and velocity is always preserved, despite the varying mechanical history preceding the stretch. The time course of the initial force response does display time-varying properties as shown in Fig. 6 and discussed below, but the final steady-state force remains essentially constant.

For the stretches shown in Fig. 5B, the final plateau levels are not exactly the same for the two plateaus. The fact that the force level was sometimes lower probably indicates a difference in excitatory drive. The variation in plateau level is shown in Figs. 2 and 4, and the data shown in Fig. 5B fall within the range of variance in these figures.

**Time course of recovery of initial stiffness**

Another feature of the force response of the muscle was the recovery of stiffness during the initial phase of the mechanical response to the second stretch. Two measurements were made on the data. The first was obtained by examining plots of $\Delta F/\Delta t$ calculated from the data of Fig. 3. The peak value of $\Delta F/\Delta t$, which for a constant velocity stretch should be related to the stiffness (if the elasticity is linear), is shown in Fig. 6A as a function of the time between the stretches shown in Fig. 3. The peak $\Delta F/\Delta t$ measured during the second stretch was reduced compared with the first stretch (which is the measured value shown at time 0 in Figs. 6, A and B) but started to recover quite quickly as the time between stretches was increased.

As a second indicator of stiffness recovery, the force increment after 0.4 mm of displacement was measured, calculated by subtracting the force recorded at the start of the second stretch from the force recorded after 0.4 mm of displacement (Fig. 6B). Measuring the force increment by this method accounted for the changing force baseline, which occurred while the muscle was being held isometric. The figure shows that the muscle stiffness (calculated for the 2nd stretch), decreased immediately after the first stretch and then started to recover quickly, reaching a new steady state value close to the control magnitude within ~30 ms.

The two measures used ($\Delta F/\Delta t$ and the force increment at 0.4-mm stretch) are simple approximations for obtaining stiffness measurements. Muscle stiffness is known to be a complex function of activation level, initial force, stretch velocity, stretch amplitude, and elapsed time. However, because the applied stretch amplitude and velocity are invariant from trial to trial, changes in stiffness observed in this study are attributable either to changes in initial force or to the passage of time. The effect of changing initial force is incorporated into the second stiffness measure, which estimates the force increment with respect to the baseline force.

The two differences between the results depicted in Figs. 6, A and B, are that the steady state was not reached until ~40 ms after the initial stretch in Fig. 6A, somewhat later.

**TABLE 1. Values of K for the steady-state interval**

<table>
<thead>
<tr>
<th>Stretch Velocity, mm/s</th>
<th>$K$, N/mm</th>
<th>± 95% CI, N/mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat 3</td>
<td>20</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>−0.013</td>
</tr>
<tr>
<td>Cat 4</td>
<td>20</td>
<td>0.060</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>−0.187</td>
</tr>
<tr>
<td>Cat 5</td>
<td>20</td>
<td>−0.310</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>−0.171</td>
</tr>
<tr>
<td>Cat 6</td>
<td>10</td>
<td>−0.377</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>−0.313</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>−0.065</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>−0.274</td>
</tr>
</tbody>
</table>

The values of $K$ were determined by fitting Eq. 4 in the text to the stretches of 4 mm in length. The ±95% confidence interval (CI) was calculated for the estimates of the slope ($K$) of force versus length.

![Fig. 2. Average force plateau values for 2 cats, divided by the initial background force (≈5 N), are plotted as a function of stretch velocity. In the cat 6 data, 4 different velocities were collected, and in cat 5, 3 velocities. Plateau force was determined as described in METHODS, and the error bars represent 1 SD.](image-url)
FIG. 3. Muscle response to 2 stretches (each 100 mm/s and 2 mm amplitude) separated by different time intervals (0–500 ms). Response to each case is an average of 2 trials.

than the measure used in Fig. 6B, and that the magnitude of the initial decrease was much greater for the measure used in Fig. 6A, an average of 36% decrease in Fig. 6A versus an average 20% decrease in Fig. 6B.

Returning to Fig. 5A, it is also noteworthy that the second stretch, when of faster velocity, evoked a sharp increase in force. However, the rate of rise of force was less rapid than that of the control stretch (occurring 500 ms after end of the 1st stretch), with a peak \( \frac{dF}{dt} \) of 350 N/s compared with 450 N/s for the control. Because measurements show a reduced stiffness during the initial portion of the second stretch in Fig. 5A, it is evident that the increase in force evoked by the ramp stretch of a faster velocity is not entirely due to the restoration of short-range stiffness but rather is dominated by the increase in velocity. Therefore, although the response to the second stretch for both cases shown in Fig. 5A appear qualitatively similar, the stiffness measurements reveal that the short-range stiffnesses were different in each case.

**Response to pulse perturbations during constant velocity stretches**

To record the time course of the mechanical properties of muscle during a stretch, a brief perturbation was applied at various points in the ramp. Provided that the experimental conditions are repeatable, the transient perturbation can also be applied in sequential trials and at varying times. As shown in Fig. 7, this method was used on a 4-mm stretch with a velocity of 100 mm/s. The trial without a pulse perturbation during the stretch was then used to calculate the response to the pulse alone by simple subtraction. The pulse perturbation was of constant amplitude in all the trials, as evidenced by the second record in Fig. 7. For the force record, the subtraction of the trial without the pulse from those with the pulse shows that the baseline of the force response to the pulse alone (4th record in Fig. 7) remained close to zero until the occurrence of the pulse. The level baseline shows that the experimental conditions were constant across all the trials until the onset of the pulse.
FIG. 5. Muscle response to 2 different stretch velocities, 100 and 20 mm/s and an amplitude of 2 mm each. Shown are averages of 2 trials. A: 1st stretch velocity was 20 mm/s and the 2nd 100 mm/s. The light line was the trial where there is no separation between the 2 stretches. Dashed line indicates the point where the velocity was changed. The heavy line was the trial where the time interval between the ramps was 500 ms. B: same as A except the velocities of the 1st and 2nd stretches were reversed.
Figure 8 illustrates the maximum force resulting from the pulse perturbation as a function of time relative to the onset of a ramp stretch. The stretch velocity was 100 mm/s in Fig. 8A and 20 mm/s in Fig. 8B, and examples from two preparations are shown in each part. The force response to the pulse applied before the start of the stretch provides the control value (i.e., the isometric response) at the starting length. Figure 8A shows that after the ramp stretch started, the force response to the pulse stretch decreases sharply and eventually reaches a minimum value in the middle of the stretch. The large force decrease elicited in response to the pulse commenced at approximately the same time as the yield, although the time course of this change is not apparent in the figure because only one pulse occurred between stretch onset and the yield point. The yield point indicated in the figure was taken to be the same as the start of the steady-state response as defined previously in Eqs. 2 and 3. After the stretch ended, the peak force elicited by each pulse increased and returned close to the prestretch (isometric) value quickly after the end of the stretch. The responses shown in Fig. 8B, which were recorded at the slower velocity, were similar to those evoked by the faster stretch. Because the stretch was slower, the time between stretch onset and the yield point was greater, hence more pulses were imposed for Fig. 8B in this time interval than in Fig. 8A. The decrease in the response in this time period was more gradual, as opposed to an abrupt discontinuity, as is shown in the figure.

It should be noted that the reason the peak force measured started to increase before the end of the stretch (last pulse before hold phase) is that the maximum force occurs sometime after the onset of the pulse, and the onset of the pulse is the variable used to plot the data. In addition, the amplitude of the pulse was > 1 mm, which is a relatively large excursion, and probably changed the mechanical properties by itself. Hence the assumption that the changes in mechanical properties due to the pulse were similar in each case is necessary. The large amplitude was essential to elicit large enough force response to record differences in force responses. Furthermore, the intent of the perturbation was to determine the stiffness of the muscle in response to a large stretch, rather than to test the response in the “small-signal” region.

DISCUSSION

Mechanical response to constant velocity stretches

The force response of the cat soleus muscle to a single constant velocity stretch is characterized by a region of high stiffness, and then by a sharp decline in stiffness, or yield. In our experiments the force after yield settled to a steady level quickly and stayed relatively constant until the end of the stretch. Furthermore, provided that the initial muscle length and background activation were held constant in different trials, the force plateau level achieved during the ramp depended solely on the velocity of stretch, and not on the recent history of length changes. Although only one initial force level was used in these experiments, the form of muscle response to large, constant velocity stretches has been shown to be consistent for a wide range of initial forces, when the crossed-extension reflex is used to activate the soleus (Boskov 1990). In fact, in the other study, plots of our experiments the force after yield settled to a steady level quickly and stayed relatively constant until the end of the stretch. Furthermore, provided that the initial muscle length and background activation were held constant in different trials, the force plateau level achieved during the ramp depended solely on the velocity of stretch, and not on the recent history of length changes. Although only one initial force level was used in these experiments, the form of muscle response to large, constant velocity stretches has been shown to be consistent for a wide range of initial forces, when the crossed-extension reflex is used to activate the soleus (Boskov 1990). In fact, in the other study, plots of the force response to a constant amplitude constant velocity stretch overlap when normalized for the initial background force.

Although the appearance of the force plateau after yield in the cat soleus (shown here) is remarkably similar to that of tetanized frog single muscle fiber data (Flitney and Hirst 1978; Harry et al. 1990; Lombardi and Piazzesi 1990), previous data from the cat soleus literature do not show a force plateau as clearly but instead show a large decrease in force during the ramp, followed by a steady rise (see for example Fig. 3 from Joyce et al. 1969). There are a number of possible explanations for these differing appearances of the force record during ramp stretch in the two preparations.

The most probable explanation for the differences in force response in the different preparations is that the methods of activation of the soleus were different: electrical stimulation in the Joyce et al. (1969) experiments and the
The crossed-extension reflex used in our experiments provides a natural activation of the muscle. Comparison of our findings with those derived from the electrical stimulation regimen used in Joyce et al. is difficult because some of the rates used in that study were unphysiologically low. This rate comparison is particularly important because the form of the force response in the Joyce et al. data depended greatly on the frequency of neural activation. Matching background force levels from the two studies reveals that the activation in our experiments corresponds approximately to a stimulation rate of \(<5\) pps in Joyce et al. It is likely that \(5\) pps is well below the normal minimum rate of activation of even slow twitch units, such as those in the soleus, and this may explain the abrupt decrease in force after the yield that is visible in much of the published cat data.

**Role of tendon elasticity**

Skeletal muscle consists of muscle fibers with contractile, viscous, and elastic properties, in series with a tendon that is primarily elastic in nature. During abrupt length changes, the net stiffness would be generated by these two elements in series, and the resulting force response would be dominated by the more compliant element. For the initial phase of the stretch response, the short-range stiffness would jointly reflect tendon and cross bridge properties, with the ratio determined by the level of activation. (At low initial forces, tendon is the more stiff, whereas at higher forces, muscle fiber short-range stiffness approaches and may exceed that of the tendon.) Once the amplitude range of cross bridge attachment (i.e., the short range stiffness) is exceeded, the resulting force profile is governed primarily by the more compliant mechanical properties of muscle. It follows that the key qualitative features of the force responses described here are not governed by tendon mechanics, although the quantitative characteristics are certainly impacted by tendon mechanical properties.

**Muscle viscouslike behavior**

The finding that the plateau force depended largely on the stretch velocity indicates that lengthening muscle behavior after a yield is analogous to that of a mechanical viscous damper, whose force response is determined solely by the velocity. Table 1 shows that this analogy is very accurate for two of the preparations. For the other two preparations, additional elastic contributions to total muscle force are more evident, although viscous behavior is still dominant at faster velocities. For a given stretch velocity, the force response achieved the same plateau level, regardless of whether the amount of time between the two stretches or the magnitude of the muscle force when the second stretch was initiated (Figs. 3 and 4). The application of a second stretch of a different stretch velocity also shows that prior movement history did not have any major effect on the viscous like behavior (Fig. 3). Although precise comparisons to force velocity relationships reported by others cannot be
Revised description of yielding behavior

The existence of yielding and short-range stiffness in muscle has been demonstrated in numerous studies and explained by the cross bridge model. Yet there has been no objective definition of when yield occurs; only the qualitative one of the point where the rate of force rise decreases. Figure 5 poses problems for even this qualitative definition. The imposition of a faster stretch immediately after the end of the first stretch induces a further increment in force, and the decrease in the force derivative during the second stretch would be called the yield point with this definition of yield. Yet, as discussed in RESULTS, the increase in force and the sharp corner, traditionally termed the yield, are not due to the restoration of a short-range stiffness. Moreover, after the initial portion of the first stretch, existing cross bridges formed in the isometric state have presumably ruptured, and another yield cannot be taking place, at least according to the classical cross bridge mechanics definition of yielding.

The important feature of data obtained from the experiments with two sequential stretches is that although the initial stiffness varies with recent movement history (as in Fig. 3), there is always a clear corner, or discontinuity in the rate of force rise, and this corner defines the beginning of the plateau, or steady-state response. Yet this steady-state viscoelastic response is separate and distinct from the initial short-range stiffness, and the transition from these two regions of behavior is almost instantaneous for fast speeds of stretch (i.e., Fig. 1). Hence we assert that the yield, or “corner” in the force record, is primarily a manifestation of the muscle’s steady-state velocity sensitivity.

Although the steady-state force response is dominated by muscle viscosity, lengthening muscle is by no means an ideal viscous element, which can be seen by the fact that the force increase is not instantaneous when the velocity is increased, including the change from zero velocity (isometric state). This observation leads to revised descriptions of both yield and short-range stiffness. For a given activation level, the number of attached cross bridges asymptotically reaches an equilibrium that depends on the velocity of stretch and the muscle length. At this point, application of a change in velocity will disrupt the cross bridge equilibrium, after which the cross bridge number is reset rapidly to a level appropriate for the new steady state. However, because the muscle stiffness is also dependent on the mean number of attached cross bridges, it follows that the stiffness would be expected to vary in conjunction with the change in velocity as well. Therefore the yielding process could simply be described as the breakdown of the elastic
properties in one steady state before establishing a new set of properties in another steady state.

An alternative hypothesis is one described by Morgan (1990), which supposes that yielding of muscle is not homogeneous and is unevenly distributed across different sarcomeres in-series. According to Morgan's hypothesis, the yieldlike response shown in Fig. 54 could be attributed to delayed yielding of sarcomeres that had not yielded originally, instead of resulting from a change in the steady-state velocity-sensitive force response. The applicability of Morgan's hypothesis to the data presented here depends on whether the stretches applied (2 mm in length) had indeed ruptured all the sarcomeres or some still remained intact. Unfortunately, not enough information is available from these experiments to determine the validity of either hypothesis. However, the conclusions concerning viscouslike steady-state behavior do not rely on the mechanism through which it is expressed; they are based simply on the relation between force and velocity.

The significant time constants involved with the transition from one steady-state response to another (as shown in Fig. 5) may well be dominated by the elastic properties of the first steady state, hence it is important to note that transient perturbations, such as white noise inputs, may elicit essentially elastic behavior. For example, white noise perturbations that have high bandwidths still show large elastic contributions to total force (Kirsch and Rymer, unpublished data), although the application of higher velocities, which result from the high frequencies, should produce larger viscous contributions. Moreover, the value of the viscous coefficient decreases with increasing bandwidths (Kirsch and Rymer, unpublished data), further supporting the idea that the higher frequencies do not allow steady-state viscous properties to be fully manifested.

**Time-dependent properties of muscle force after completion of the initial yielding stretch**

Figure 6 shows that the recovery of the stiffness measurement in the isometric state after a yielding stretch took place rather quickly, within 30–40 ms, and this result may be an important intrinsic feature of muscle. Virtually any elapsed time interval with the muscle held in an isometric state gives the muscle opportunity to recover short-range stiffness. Therefore, if a muscle is stretched beyond the point of yield, the muscle can reset to its original mechanical state in a very short amount of time and can do so without any reflex assistance (although reflexes may well accelerate this recovery process). The implication of this result in relation to reflex action will be discussed in a following section. The amount of time for recovery in the soleus is 30–40 ms as shown in Fig. 6, and it could be appreciably faster for other muscles with fast-twitch muscle fiber types.

**Time-dependent mechanical properties during a ramp stretch**

The transient pulse stretch applied during the ramp stretch was intended to be an approximation of a mechanical impulse. Although the peak force measurement was an incomplete description of the whole mechanical impulse response function, it conveniently provided a single number to characterize the mechanical response as a function of time. In Fig. 8 we showed that, although the overall force was still increasing in response to the stretch in the short-range stiffness region, the mechanical response to the pulse immediately declined, because of movement onset. However, once the decline was complete, the mechanical response remained near the minimum level until the end of the stretch. This may indicate that the equilibrium between attachment and detachment of cross bridges, which depends on the velocity of stretch, has already been reached, thereby producing a constant mechanical response. This conclusion is in agreement with the response to stochastic length perturbations of the soleus, which could be modeled quite accurately by a simple linear first-order model once the muscle had yielded (Kirsch and Rymer, unpublished data). Hence, although a discontinuity in muscle properties has been traversed, the "new" muscle mechanical properties are relatively simple.

**Implications for reflex/neural control of muscle**

As discussed in the introduction, yielding of muscle occurs too rapidly for conventional feedback control schemes to compensate for the yield and preserve the elastic behavior. Hence it is likely that a predictive or anticipatory control algorithm is being implemented by the reflex system. For such an algorithm to be effective, it is necessary that the initial behavior of the muscle be stereotyped, because the algorithm is predicting future events on the basis of the present states. Short-range stiffness is an example of stereotyped behavior that enables predictive schemes to be successful. Yet measures of stiffness in areflexive muscle do vary with the amount of elapsed time after the muscle has reached an isometric condition. But, because the time course of stiffness recovery is very fast, such that stiffness is restored within 30–40 ms of acquisition of the isometric state, the plant does maintain the necessary characteristics for a predictive control scheme to be effective.

The results of our experiments have shown that after a yield, areflexive muscle shows simple viscouslike properties during a stretch. Because viscosity promotes stability under all types of loads, the mechanical properties of muscle can only help promote stability, even after the yield. This is significant for cases in which the velocity of stretch is very fast so that yielding of muscle does occur, even when the stretch reflex is intact. The viscouslike property promotes stability until the stretch reflex has time to compensate for the nonlinear behavior due to yielding. In addition, our finding that the steady-state viscouslike behavior in response to constant velocity stretches is not influenced by prior mechanical history is important. The control strategy for specifying the requisite muscle activation is simplified by this fact, because the intrinsic muscle performance even after yield is predictable and not dependent on the preceding movements. It should be noted, however, that the path taken by the muscle to reach the steady-state force level does vary with movement history.

Last, the observation of viscouslike properties of postyield lengthening muscle are consistent with those current theories of stretch reflex function that propose that
the stretch reflex regulates the stiffness of the muscle. Specifically, it has been shown elsewhere (e.g., Nichols and Houk 1976) that reflexively active muscle remains remarkably elastic in the face of a broad range of perturbations; but the new idea presented in this paper is that the stretch reflex does not simply preserve elastic behavior. Instead, the stretch reflex changes the form of the mechanical force response from one dominated by viscosity to one dominated by elasticity, similar to that exhibited by muscle before the yield. Therefore the reflex acts to preserve the system's elasticity, which is functionally significant in those situations where posture and position control are important.

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